DISTIGOUANIA IRREGULARIS (RHAMNACEAE) GEN. ET SP. NOV. IN MID-TERTIARY AMBER FROM THE DOMINICAN REPUBLIC

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ABSTRACT

Distigouania irregularis (Rhamnaceae) is described as a new genus and species of fossil angiosperm from deposits of Mid-Tertiary amber in the Dominican Republic, on the Caribbean island of Hispaniola. The fossil is represented by a single staminate flower at anthesis and displays an irregular corolla in which 4 petals are rhombic-lanceolate, spreading, and sepal-like, while the 5th is shorter, erect, and slightly cupped. The stamens are dimorphic; the 4 that are opposite the spreading petals have dehisced anthers on erect filaments that diverge from the petals, while the 5th stamen adjoins the erect, cupped petal and has a larger, unopened anther. The hypanthial disc is densely pubescent with tangled trichomes, and on the disc margin, at the base of each sepal, is an enlarged, bilobed, probably glandular appendage. There are minute papillate trichomes on the disc appendages and on the epidermis of the anthers. These epidermal papillae, as well as the pubescent disc and bilobed appendages, are similar to features of staminate flowers in various extant American species of *Gouania*. However, the fossil is unique within family Rhamnaceae in its irregular corolla and androecium, and it stands out as an evolutionary experiment with zygomorphy in this otherwise actinomorphic family.

RESUMEN

Distigouania irregularis (Rhamnaceae) se describe como género y especie nuevos de angiosperma fósil de los depósitos de ámbar del Terciario medio de la República Dominicana, en la isla caribeña de La Española. El fósil está representado por una flor simple estaminada en antesis que muestra una corola irregular cuyos cuatro pétalos son rómbico-lanceolados, patentes, y semejantes a sépalos, mientras que el quinto es más corto, erecto, y ligeramente acopado. Los estambres son dimórficos; los 4 que están opuestos a los pétalos desplegados tienen anteras abiertas en filamentos erectos que divergen de los pétalos, mientras que el quinto estambre se acerca al pétalo erecto acopado, y tiene una antera más grande no abierta. El disco hipántico es densamente pubescente con tricomas enmarañados, y en el margen del disco, en la base de los sépalos, está un apéndice ensanchado bilobulado, probablemente glandular. Hay tricomas con papilas diminutas en los apéndices del disco y en la epidermis de las anteras Estas papilas epidérmicas, así como el disco pubescente y los apéndices bilobulados, son similares a las características de las flores estaminadas de varias especies americanas actuales de *Gouania*. Sin embargo, el fósil es único en la familia Rhamnaceae por su corola irregular y androceo, y se mantiene como un experimento evolutivo con la zigomorfía en esta familia actinomórfica por lo demás.

INTRODUCTION

Amber mines in the mountains of central Hispaniola have yielded numerous fossil flowers from Mid-Tertiary tropical forests in the Caribbean region. The present flower is the 16th species to be described from these deposits. Others are 1 species of Fabaceae (Poinar 1991), 3 of Arecaceae (Poinar 2002a, 2002b), 2 of Poaceae (Poinar & Judziewicz 2005; Poinar & Columbus 2012), 1 of Chrysobalanaceae (Poinar et al. 2008a; revised by Chambers & Poinar 2010), 2 of Lauraceae (Chambers et al. 2011a, 2012), 3 of Meliaceae (Chambers et al. 2011b; Chambers & Poinar 2012), 1 of Burseraceae (Chambers & Poinar 2013), 1 of Myristicaceae (Poinar & Steeves 2013), and 1 possibly of Moraceae (Poinar et al. 2008b). The moist forests of this period have been described by Poinar and Poinar (1999), based on numerous amber-embedded insect species together with whatever plant fossils were then available. The resin that trapped these organisms was produced by *Hymenaea protera* Poinar (Poinar 1991), a progenitor of the modern-day forest species *H. courbaril* L. Fossils of Rhamnaceae, principally leaves and fruits from the Late Cretaceous and Early Cenozoic, have been the object of numerous studies (see references in Jones & Dilcher 1980; Burge & Manchester 2008; Correa et al. 2010) and have contributed to phylogenetic and historical phytogeographic analyses of the family (Richardson et al. 2000a, 2000b, 2004).

MATERIALS AND METHODS

This and the other fossils referred to above were collected from amber mines in the Cordillera Septentrional, between Puerto Plata and Santiago, Dominican Republic. Different dates have been ascribed to the marine sediments in which the amber is found. A younger proposed age of 20–15 Ma is based on foraminifera present in the deposits (Iturralde-Vinent & MacPhee 1996). An older age of 45–30 Ma is based on marine coccoliths (Cépek in Schlee 1999). The amber is in turbiditic sandstones of the Upper Eocene to Lower Miocene Mamey Group (Draper et al. 1994). Examination and photographs were made with a Nikon stereoscopic microscope SMZ-10-R at 80× and a Nikon Optiphot microscope at 800×.

DESCRIPTION

Distigouania K.L. Chambers & Poinar, gen. nov. (**Figs. 1–5**).TYPE SPECIES: *Distigouania irregularis* K.L. Chambers & Poinar, sp. nov.

Flower staminate, pedicel glabrous, hypanthium dish-shaped, glabrous (Fig. 5), calyx radially symmetrical, sepals 5, equal, spreading (Fig. 1), corolla irregular, with 4 spreading, petals, not cupped or hooded, and 1 shorter, cupped, erect petal (Figs. 1, 3, 4), stamens dimorphic, the 4 opposite the spreading petals erect on slender filaments, with dehisced, bilocular anthers, stamen opposite the cupped petal with the anther larger, ± appressed to petal, indehiscent or possibly tardily dehiscent, disc flat, densely pubescent with tangled trichomes (Fig. 2), appendages of disc 5, enlarged, bilobed, each opposite the base of a sepal (Fig. 2), epidermis of disc appendages and anthers minutely papillate, style none. Pistillate flower unknown.

Etymology.—From Latin "disto," to stand apart, be separate, and *Gouania*, a genus of Rhamnaceae.

Distigouania irregularis K.L. Chambers & Poinar, sp. nov. TYPE: HISPANIOLA. DOMINICAN REPUBLIC: amber mine in the northern mountain ranges (Cordillera Septentrional), 1998, *unknown amber miner s.n.* (HOLOTYPE: catalogue number Sd-9-178, deposited in the Poinar amber collection maintained at Oregon State University, Corvallis, Oregon 97331, U.S.A.)

Sepals glabrous, ovate, 0.9–1.2 mm long, 0.7–0.8 mm wide, tip acute to acuminate, not thickened, midline ridged (Figs. 1, 2), corolla glabrous, the 4 spreading petals rhomboid-lanceolate, 0.7–0.9 mm long, 0.4–0.5 mm wide, acute (Fig. 1), 5th petal obovate, obtuse, ca. 0.4 mm long, 0.35 mm wide, slightly cupped (Figs. 1, 3, 4), filaments of 4 erect, dehiscent stamens 0.014–0.027 mm long, valves of dehisced anthers 0.023–0.030 mm long, 0.013–0.018 mm wide (Figs. 2, 3), undehisced anther valves of 5th stamen ca. 0.032 mm long, 0.022 mm wide (Fig. 3), filament of undehisced anther ca. 0.015 mm, disc appendages 0.025–0.028 mm wide, 0.018–0.022 mm long (Fig. 2), pedicel 1.2 mm long.

Etymology.—From Latin "irregularis," divisible into 2 equal halves along one plane only.

DISCUSSION

Our original comparison of the fossil was with *Gouania*, a pantropical genus of ca. 50 species (Medan & Schirarend 2004; Pool 2014). Examination of published illustrations and a limited sample of herbarium specimens has not shown any examples of irregular corollas or anthoecia, nor do standard descriptions of the genus mention these floral features. In such a large genus, it is not inconceivable that irregular flowers may have evolved in some extant species; however, if present, they seem to have escaped notice. With respect to a shallow hypanthium, small petals cupping the anthers, a flat, pubescent disc, bilobed disc appendages, and lack of a style in staminate flowers, the fossil resembles *Gouania* taxa such as *G. hypoglauca* Standl., a Central American species. A review of *Gouania* in the Caribbean, Mexico, and Central America was recently published by Pool (2014), giving a basis for comparing *Distigouania* with modern species of this region. Treatments of the Rhamnaceae as a whole (e.g., Sussenguth 1953; Medan & Schirarend 2004) describe the family as having radially symmetrical flowers. This fossil is so unusual in its floral structure, therefore, that we believe it merits description as a separate genus.

A feature of the flower not yet remarked on is the strong similarity of the 4 laterally spreading petals to the sepals. Except for being smaller, these petals are like the sepals in their shape and textural appearance, as fossilized. Their color, in life, may also have been sepal-like. A further similarity is the presence of a partial mid-

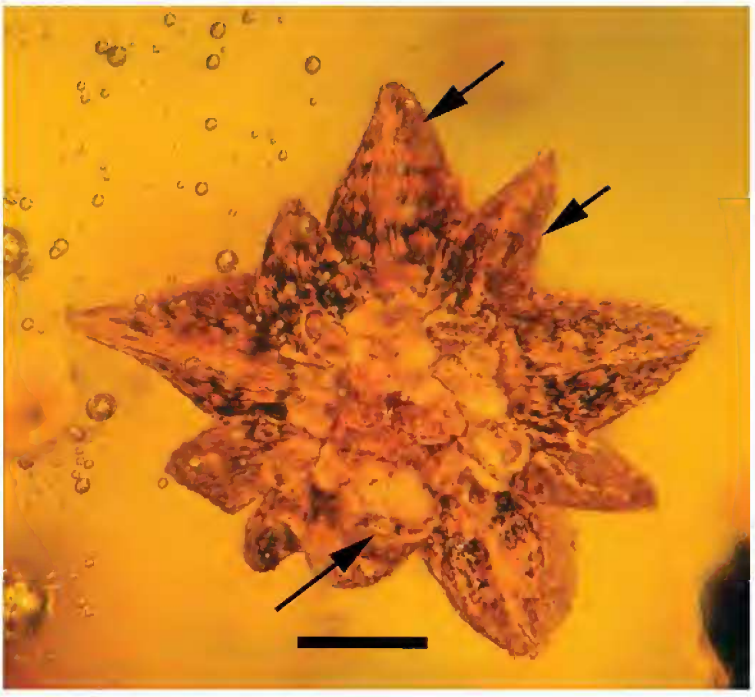

Fig. 1. *Distigouania irregularis*. Apical view of flower. Upper arrow is on sepal, middle arrow indicates one of the 4 spreading petals, lower arrow shows erect, cupped petal. Note ridge on sepal midline. Scale bar = 0.7 mm.

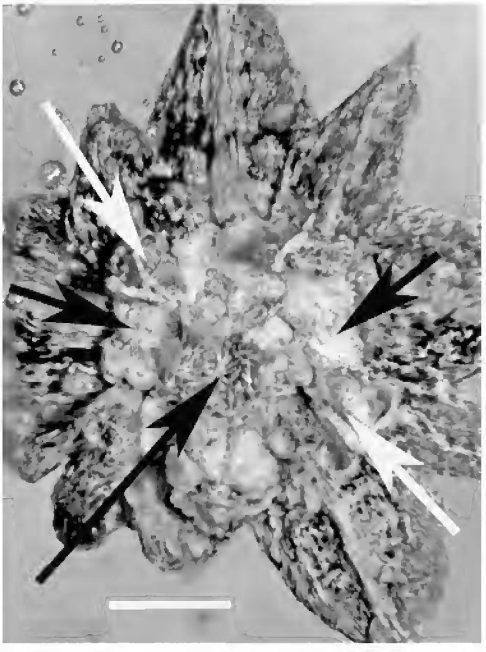

Fig. 2. *Distigouania irregularis*. Enlarged apical view. Long black arrow indicates tangled trichomes on hypanthial disc, 2 short black arrows are on bilobed disc appendages, white arrows point to 2 dehisced anthers. Scale bar = 0.49 mm.

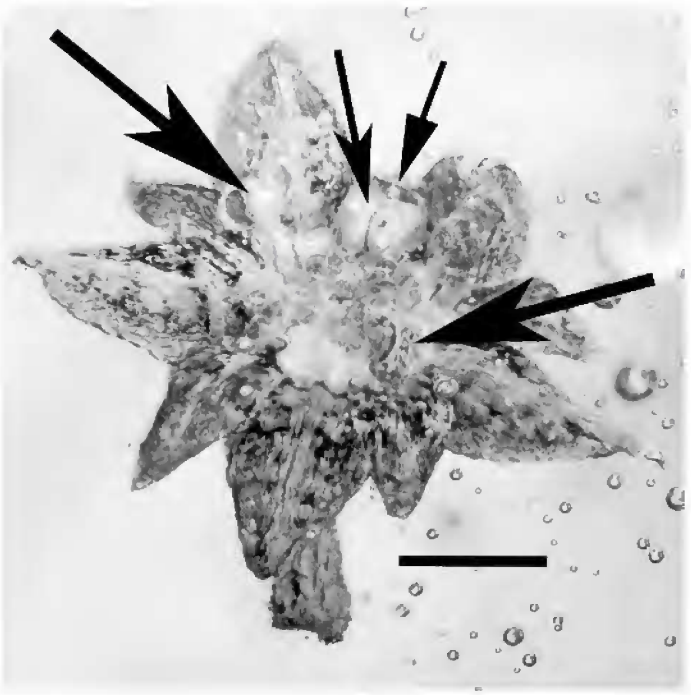

Fig. 3. *Distigouania irregularis.* Apical view. Long arrows are on dehisced anthers, short arrow, top middle, points to undehisced anther, shortest arrow, top right, indicates cupped petal subtending this anther. Scale bar = 0.675 mm.

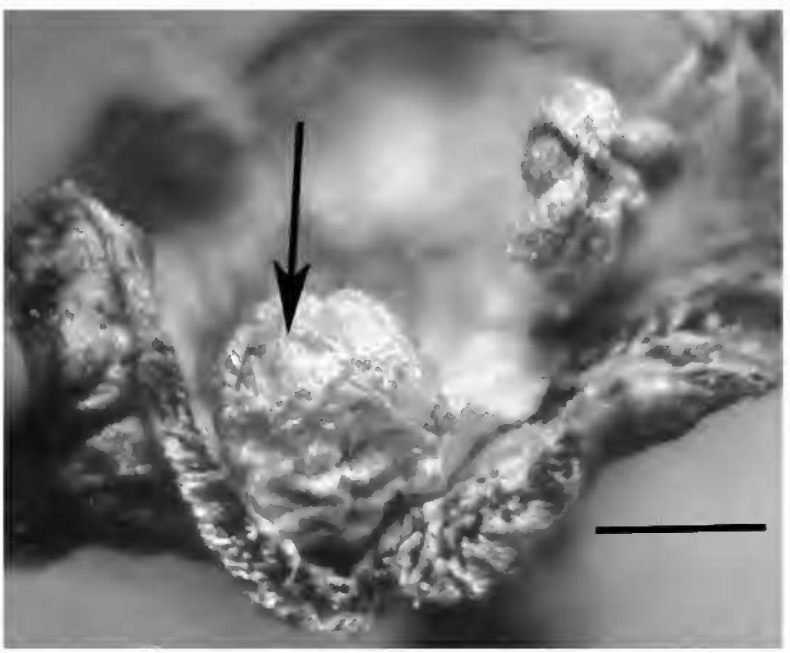

Fig. 4. *Distigouania irregularis.* Lateral view. Arrow indicates the erect petal, which is cupped and subtends the stamen with undehisced anther. Scale bar = 0.26 mm.

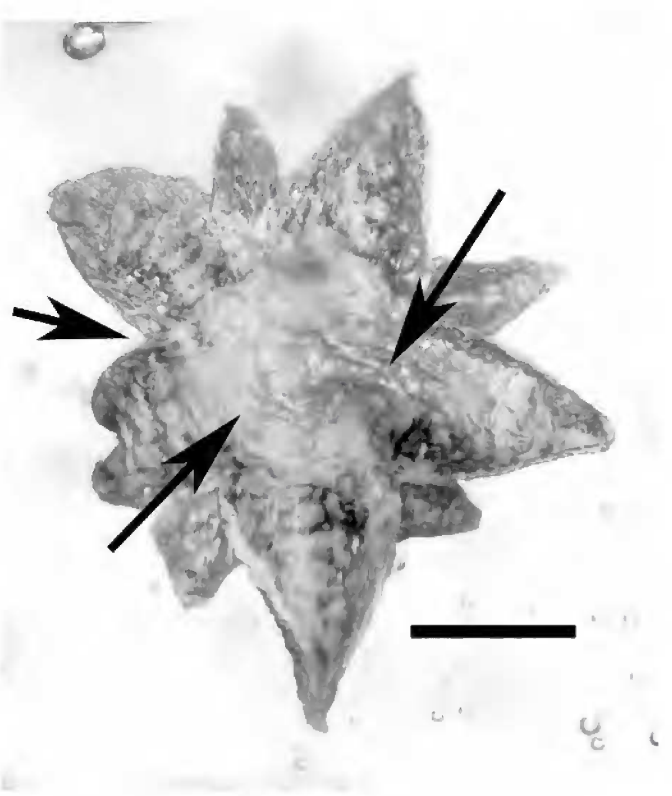

FIG. 5. *Distigouania irregularis*. Basal view. Right arrow is on pedicel, upper left arrow indicates location of 5th, non-spreading petal, lower arrow is on hypanthium. Scale bar = 0.736 mm.

line ridge, visible in the proximal half of petals in the 2 o'clock and 4 o'clock positions in Figure 1. The 5th petal, erect and cupped against the undehisced anther (Fig. 1, lower arrow, Fig. 4) is like the limb of a typical petal of Rhamnaceae in size, shape, and texture. At a developmental- genetic level we speculate that the sepaloid appearance of 4 of the second whorl organs could result from the partial loss of expression of B class genes in this whorl (from the ABC model of flower development, see Bowman et al. 1989; Theissen et al. 2000), as occurs in a variety of extant taxa (e.g., Kramer et al. 2003). Additionally, loss of radial symmetry and petal showiness could result from changes in the expression pattern of flower symmetry genes (Preston et al. 2011). Therefore, if extant members of Rhamnaceae with a similar phenotype were found, it could lead to interesting comparative studies of the genetics of candidate genes for flower development, such as orthologs of *PISTILLATA, APETALA3, CYCHLOIDEA* and *DICHOTOMA*. We might then come closer to explaining the morphology of this unusual Mid-Tertiary fossil.

If allied to *Gouania*, as hypothesized, *Distigouania* is a member of Tribe Gouanieae (Richardson et al. 2000a:333; Medan & Schirarend 2004:330). In a molecular phylogenetic analysis of Rhamnaceae using the plastid genes *rbcL* and *trnL-F*, Richardson et al. (2000b) found 3 well-supported clades; however, these could not be characterized morphologically, at least with presently available data. They were given the informal names of the *rhamnoid clade*, the *ampeloziziphoid clade*, and the *ziziphoid clade*. Gouanieae belong to the *ziziphoid clade* as a well-supported, monophyletic group, consisting of *Crumenaria, Gouania, Helinus, Pleuranthodes*, and *Reissekia*. In their discussion of the biogeography of Rhamnaceae, these authors propose a phylogeny extending back to the Mid-Cretaceous with possible relationships to the Rose Creek flower of Basinger and Dilcher (1984), which may establish 94–96 Ma as the minimum age of the family.[1] For some genera, at least, a

[1]Assigning the Rose Creek flower to Rhamnaceae is not accepted by some other authorities, however (Calvillo-Canadell & Cevallos-Ferriz 2007:1667).

widespread Old and New World distribution may be attributed to their ancestors' initial presence in Gondwanaland prior to its breakup. The occurrence of modern genera of Rhamnaceae in the late Cretaceous has not yet been firmly established in the fossil record. Flowers of this family, not specifically assignable to an extant genus, were discovered in Mexican strata of probable late Campanian age, ca. 74 Ma (Calvillo-Canadell & Cevallos-Ferriz 2007). Upper Maastrichtian leaves of *Berhamniphyllum* (Jones & Dilcher 1980; Correa et al. 2010) are similar to those of *Rhamnidium* and *Berchemia*, while the winged fruit of *Archeopaliurus* (Correa et al. 2010) compares well with that of *Paliurus*. Taking into account both fossil and molecular evidence, Calvillo-Canadell and Cevallos-Ferriz (op. cit.) propose an Eocene/Oligocene origin for genera such as *Gouania, Ziziphus, Berchemia, Karwinskia*, and *Paliurus*.

The present fossil, from the Oligocene or early Miocene, stands out as an evolutionary experiment with zygomorphic flowers in this otherwise actinomorphic family. Because floral zygomorphy is frequently associated with insect pollination, we suggest that the notably enlarged, bilobed appendages of the hypanthial disc may have been nectariferous, supplying a reward for insect visitors. The function of the undehisced anther, which stayed closed while the other 4 anthers opened and released their pollen, remains unexplained. Given the absence of living relatives having a comparable floral syndrome, we choose not to speculate on whether, in this species, it also may have had a particular function in insect pollination.

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